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Morphospace expansion paces taxonomic diversification after end Cretaceous mass extinction

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Abstract

Highly resolved paleontological records can address a key question about our current climate crisis: How long until the biosphere rebounds from our actions? There are many ways to conceptualize the recovery of the biosphere; here we focus on the global recovery of species diversity. Mass extinction may be expected to be followed by rapid speciation, but the fossil record contains many instances where speciation is delayed, a phenomenon for which we have a poor understanding. A likely explanation for this delay is that extinctions eliminate morphospace as they curtail diversity, and the delay in diversification is a result of the time needed for new innovations to rebuild morphospace which can then be filled out by new species. Here, we test this Morphospace Reconstruction Hypothesis using the morphological complexity of planktic foraminifer tests after the Cretaceous-Paleogene mass extinction. We show that increases in complexity precede changes in diversity, indicating that plankton are colonizing new morphospace and then slowly filling it in. Preliminary diversification is associated with a rapid increase in the complexity of groups refilling relict Cretaceous ecospace. Subsequent jumps in complexity are driven by evolutionary innovations (development of spines and photosymbionts) which opened new niche space. The recovery of diversity was paced by the construction of new morphospace, implying a fundamental speed limit on diversification after an extinction event.

Introduction

Although present rates of extinction do not (yet¹) rival the Big Five mass extinctions, humanity is undeniably causing elevated rates of biodiversity loss through climate change, habitat destruction, invasive species introduction, etc.¹ As we seek to mitigate this loss, we must also learn how long it will take for biodiversity and ecosystem functionality to recover after negative anthropogenic effects subside. The Cretaceous-Paleogene (K-Pg) mass extinction, caused by the impact of an asteroid on the Yucatán Platform in the southern Gulf of Mexico², is the most recent and most rapid of the five major mass extinctions and is perhaps the only major event in Earth history which happened faster than modern climate change. Thus, it provides a unique analog for future recovery from rapid extinction.

Following the geologically-instantaneous disappearance of a huge portion of the biosphere, it may be presumed that survivors would rapidly diversify to fill empty ecospace. The global recovery of planktic foraminiferal diversity following the K-Pg mass extinction is a classic example of such explosive adaptive radiation³⁻⁷. Survivor species, adapted for shallow water and marginal marine environments, gave rise to dozens of new taxa which recolonized the open marine ecospace vacated by the extinction event^{4,5,8-12}. This explosive radiation occurred in several pulses, the latter of which were delayed for millions of years^{3,13-14}. The initial early Danian burst in diversity only added about twenty species, less than a quarter of pre-extinction diversity¹¹. Global richness increased unsteadily throughout the Paleocene, and did not begin to approach even mid-Cretaceous levels until the Paleocene-Eocene boundary, 10 myr later (Fig. 1A). The full recovery of species- or genus-diversity took more than 20 myr, into the middle Eocene¹⁸, at which point it nearly matched the soaring heights of the Late Cretaceous.

Genus-level macrofaunal diversity data shows that a 10-myr delay in elevated rates of origination is a feature of all mass extinctions, including the K-Pg¹⁵⁻¹⁷. This delay has also been identified in marine plankton after the K-Pg (Fig. 1A)¹⁸⁻²⁰, although its cause remains unknown. Explanations have tended toward external environmental controls like the delayed recovery of marine export production⁴, or the persistence of toxic metals or other lingering stressors affecting conditions in the upper water column well after the extinction²¹ possibly driven by Deccan Volcanism²²⁻²⁵. Productivity, however, was highly variable in the early Paleocene, with some localities showing a geologically-immediate increase after the extinction²⁶. Even considering the longest possible delay in the recovery of global export productivity and the recolonization of deeper habitats¹³⁻¹⁴, about 4 myr, this still does not provide a satisfying explanation for why diversity might remain low for so much longer, up to 20 myr. No evidence of toxic metal enrichments has been found in early Paleocene sediments, and recent work within the Chicxulub Crater, where impact-driven environmental contamination would be worst, documented a rapid recovery there¹². The lack of a discernable environmental driver has led many authors to propose that ecology, rather than environment, controls diversification after a mass extinction^{12,26-27}.

An important ecological control on diversification could be the time needed to reconstruct morphospace within ecosystems¹⁶, which we term the Morphospace Reconstruction Hypothesis. We often conceive of post-extinction radiations refilling empty niche space, but as Kirchner and Weil¹⁶ pointed out, the reduction of diversity caused by mass extinctions also destroys niche space (see also Erwin's excellent review²⁸). Although ecological niches can be conceptualized as slots in an ecosystem which different organisms can fit into, they are actually created by and are thus inseparable from the organisms which occupy them. In other words, organisms themselves construct the environments they inhabit²⁸. This can be more properly conceived of as morphospace

(i.e., the range of morphologies occupied by a clade), which represents the range of successful strategies that a clade has made to adapting to its environment and pressure from other organisms²⁸. “Ecological niches” are a simplified but handy way of conceptualizing this range of successful adaptations.

Newly colonized morphospace can serve as a jumping-off point for further evolutionary innovation, which in turn opens additional ecospace, and so on, until a clade reaches its limits. Thus, once existing niches are full, additional diversification is dependent on evolutionary innovations to open new niche spaces, a concept borne out by modelling studies^{19,20}. The time required to rebuild morphospace is an attractive explanation for the delayed recovery of taxonomic diversity following the K-Pg mass extinction. A large volume of literature has shown that, generally, morphological innovation is expected to lead diversity during radiations, including after mass extinctions^{28,31-33}. But these have dealt primarily with higher orders of taxa, had limited temporal resolution, and, to our knowledge, have not explicitly tested the hypothesis that morphospace reconstruction is a limiting factor in diversification. Here, we use a highly resolved (both temporally and taxonomically) fossil dataset, the species-level diversity and morphological complexity of planktic foraminifera after the K-Pg mass extinction, to test the Morphospace Reconstruction Hypothesis.

Complexity (here similar to disparity; see Methods) is calculated from a dataset of ten parameters attempting to capture the large-scale trends in the morphological evolution of the foraminifer test. The simple ‘survivor taxa’ of the immediate K-Pg recovery had simple morphologies and broad ecological niches^{7,9,34}. Planktic foraminifera may be considered an analog for other zooplankton and larger organisms in the upper ocean which are not as well represented in the fossil record.

If diversification is delayed because of the need for new innovations to open new ecospace, we expect 1) that complexity recovers before diversity, 2) diversification to be associated with large jumps in complexity, suggesting morphospaces are colonized first, and then filled, 3) throwback-type ecospace (i.e., trophic strategies of Cretaceous survivors) to be refilled rapidly after the extinction and then stabilize, and subsequent diversification/increases in complexity to be associated with evolutionary innovations opening new morphospace.

Results/Discussion

There is a massive drop in mean morphologic complexity at the K-Pg boundary which is evident however complexity is plotted, whether mean or median complexity (Fig 1B), total complexity/diversity (Fig. 1C), or complexity by trophic strategy (Fig. 1D). Unlike diversity (Fig 1A), however, morphologic complexity rebounds more quickly, reaching a plateau near its post-extinction maximum within ~ 5 myr. This is roughly coincident with an increase in planktic foraminifer diversity, and is ~1 myr after the final recovery of surface to deep $\delta^{13}\text{C}$ gradients³ and the marine carbon pump³⁵. The recovery of morphological complexity indicates that the morphospace occupied by planktic foraminifera has been rebuilt to roughly Cretaceous values.

To understand why morphologic complexity recovers before diversity, we plot them together as mean complexity/diversity (Fig. 1C). If morphospace expands at roughly the same rate as diversity, the mean complexity/diversity timeseries is a flat line; if morphospace is colonized first and then filled out (i.e., new, more complex species colonize a new ecospace, driving increases in mean complexity) then the mean complexity/diversity timeseries will have a very steep positive slope. This makes mean complexity/diversity the degree of partitioning in the morphospace. The nearly flat line in the Late Cretaceous (Fig. 1C) shows that this interval was characterized by matching increases in complexity and diversity filling out existing morphospace. In the Paleocene,

however, morphologic complexity significantly outpaces diversity. We observe three distinct intervals of increased complexity/diversity in the Paleocene (numbered in Fig. 1C), the latter of which are dwarfed by the huge peak in the basal Paleocene. Each of these intervals coincides with an interval of increasing diversity (the climaxes of which are marked with dashed lines on Fig. 1). This is consistent with the observation that morphological complexity tends to increase before taxonomic diversity during radiations³¹⁻³³. Interestingly, the Eocene is associated with roughly flat complexity/diversity, indicating a return to more linear relationship between diversification and morphological change, despite continued diversification.

We can break these trends down further to understand which groups are driving change in each particular interval. Survivors from the Cretaceous were non-spinose and did not have photosymbionts⁶ and were therefore grazers, feeding on phytoplankton and organic detritus; here we call this group of foraminifera “throwback-type” since they represent the most common pre-extinction lifestyle. The appearance of spines in the basal Paleocene family Globigerinidae allowed these foraminifera and their descendants to adopt a carnivorous lifestyle, feeding on any mobile zooplankton they might snare in their rhizopodal network⁵. The later acquisition of photosymbionts in the mid Paleocene, ~ 4 myr after the K/Pg extinction, allowed those new genera to supplement their food supply in oligotrophic waters^{3,13-14}.

The initial increase in complexity/diversity was driven by both the radiation of throwback-type forms filling niches similar to those occupied during the Cretaceous and the contemporaneous radiation of spinose forms colonizing novel ecospace (Fig 1C). Subsequent pulses in complexity/diversity are associated with evolutionary innovations within the new spinose group and the appearance and radiation of symbiont-bearing planktics (Fig 1C).

Overall, our data demonstrate that the generally marginal-marine Cretaceous survivors rapidly reoccupied and diversified within the vacant open-ocean ecospace during the early Paleocene. This interval may be considered the classic “refilling” of vacant niches after an extinction event, but represents more limited morphospace occupation compared to the Late Cretaceous. Because the bulk of morphospace available to planktic foraminifera disappeared along with its inhabitants at the K-Pg boundary, there was a more narrow range of successful life strategies available to planktic foraminifera, and thus diversity at this point is much lower than it was at the end-Cretaceous. Subsequent Paleocene radiations were driven by new evolutionary innovations that opened new morphospace (i.e., pulses in complexity/diversity). This relationship confirms the hypothesis¹⁶ that the reconstruction of morphospace is a prerequisite for the recovery of diversity after mass extinctions. It also suggests a fundamental speed limit on the rate of diversification.

Throughout their history, the turnover of planktic foraminifera has been driven by both climate³⁶⁻³⁹ and more basic macroevolutionary processes related to biology and ecological interactions between organisms^{19,40}. To determine how climate may have affected the trends we observe, we compare our taxonomic and morphometric data with Paleocene-Eocene stable isotopes and key climate events. Following post-K-Pg warming, the Paleocene is characterized by a long, slow cooling and then a slightly faster (and more variable) warming trend leading into the Paleocene Eocene Thermal Maximum (PETM). This is punctuated by a few mild hyperthermal events, including the Dan-C2 event⁴¹, the Late Danian Event (LDE)⁴², and the Early Late Paleocene Event (ELPE)⁴³. Prior to the obvious turnover at the PETM^{18,37} there is no clear relationship between either planktic foraminifer diversity or morphologic complexity and any particular climate event or trend. The Dan-C2 hyperthermal occurs after the rapid diversification

of the early Paleocene, and that event only lasted 400 kyr and thus doesn't explain the diversity or complexity trends that occur after it. Likewise, our data don't support the hypothesis that Deccan Volcanism impeded the recovery of diversity²²⁻²⁵, as the initial diversification in the early Danian occurs well before the end of Deccan volcanism (Figure 2)⁴⁴ during an interval associated with environmental stress at some sites²³⁻²⁵. With the LDE we run into the limits of our bin size, as it appears that the evolution of photosymbionts coincides with this event when in reality it preceded it by ~400 kyr⁴⁵ and the radiation of this group occurs after this event⁴⁶. The ELPE occurs during a slight decline in overall diversity, but these trends extend far beyond it. Finally, the PETM clearly exerts an influence on richness at the end of the Paleocene, but this major climatic event is not associated with any changes in morphological complexity, which was already recovered by that point.

This is not to say that climate did not influence the evolution of planktic foraminifera at all through this interval (or the structure of local populations), but that its influence was less important compared to the limit imposed by morphospace occupation. The pulses of evolutionary innovation opening novel morphospace that we describe all occur prior to the obvious turnover at the PETM³⁷, and this is also (mostly) the interval of significantly elevated origination rates¹⁸. However, diversification continues into the Eocene, finally reaching roughly Late Cretaceous values ~ 20 myr after the extinction¹⁸. Significant macroevolutionary events throughout the Eocene (and later) are coincident with major climatic events, like the Paleocene-Eocene Thermal Maximum, Eocene Climate Optimum, etc.¹⁸ This suggests a two-phase period of recovery. In the first phase, the Paleocene, diversification was limited by the need to rebuild morphospace, which provided the scaffolding on which to evolve new species. Eventually, morphospace had been expanded to an extent which allowed climate to become the primary driver of diversity. Ezard et al.¹⁹ showed that

a clade's ecology is a key factor in how successful it is in diversifying during different climate states. But after a mass extinction, ecospace must be rebuilt to the point where it can respond to changes in climate. Niche space reconstruction is therefore an essential first step in recovery, and a clear explanation for the observed 10 myr delay in speciation following mass extinction^{16,17}.

The generation of novel morphospace after the K-Pg extinction represents stepwise change into a wholly new Cenozoic planktic ecosystem, rather than a return to a mirror-version of the pre-extinction Cretaceous ecosystem. This should serve as an important reminder¹⁶: some ecological niches lost due to anthropogenic climate change will never reappear. While the future biosphere may eventually regain pre-Anthropocene numerical biodiversity levels, it will be significantly different than the biosphere in which we evolved and presently co-exist. This recovery will likely take millions of years.

Figure Captions

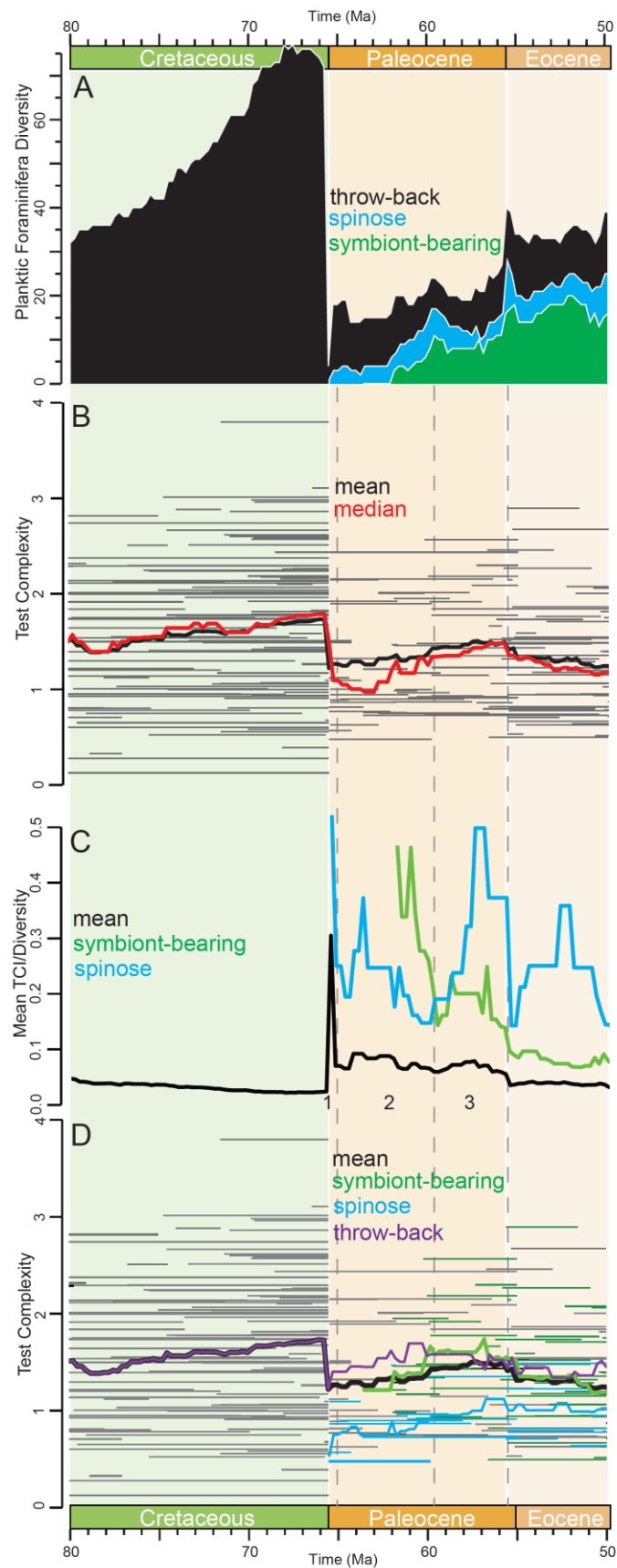


Figure 1. **A)** Planktic foraminifer diversity from the Late Cretaceous to middle Eocene. Black: throwback-type, Blue: spinose, Green: symbiont-bearing. **B)** Mean and median test complexity plotted over individual species' complexity values (horizontal lines). **C)** Mean test complexity divided by diversity. **D)** Test complexity index by trophic strategy. Grey lines on B and D are individual species. Vertical dashed lines separate the three main peaks in Mean Complexity/Diversity (numbered 1-3 in C). Possible spinose and symbiont species in the Cretaceous are lumped as “throwback” on the Cretaceous side of this plot because not all Cretaceous planktics have been evaluated for these traits. All survivor species were non-spinose and non-symbiont bearing, and thus these traits had to re-evolve anyway.

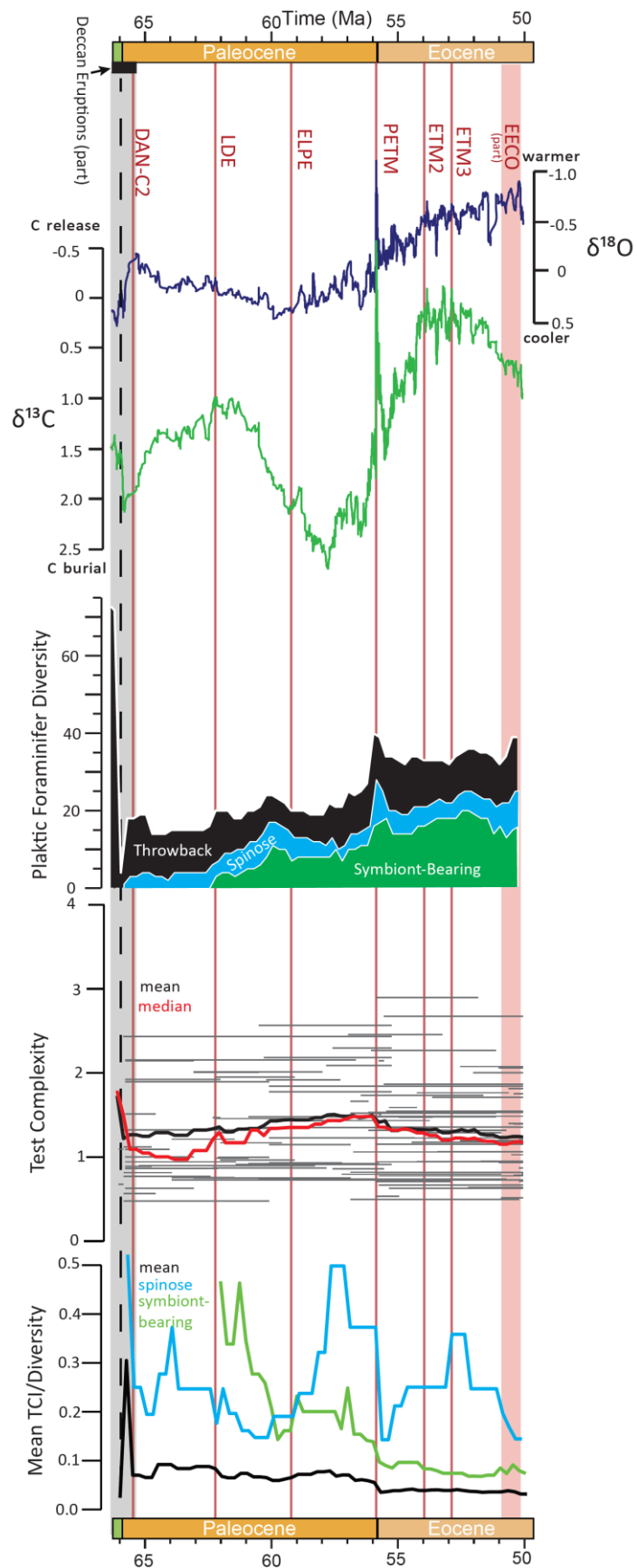


Figure 2. Comparison of early Paleogene climate events with planktic foraminifer diversity and complexity trends. Oxygen (blue) and carbon (green) isotope curves and key climate events are taken from the Geologic Timescale⁴⁷. Black bar and gray shading show the duration of post K-Pg phase of Deccan volcanism. See Figure 1 for explanation of diversity and complexity plots. Note that apparent mis-ties between boundaries and species ranges are the result the significantly higher resolution of the isotope record compared to our fossil data which is binned at 250 kyr.

Methods

Planktic foraminifer diversity data and species ranges are based on those reported in Fraass et al.¹⁸, who compiled them from community-based atlas projects⁴⁸⁻⁴⁹. Such a global compilation avoids the problems of studying the recovery of diversity/complexity at any particular site, as it avoids the range of possible local effects on species diversity, and allows direct comparison to similar global diversity records^{15,18,19,29-33,40}. The species included and their first and last occurrence datums are very similar to other recent efforts (e.g., Aze et al.⁵⁰). Morphological complexity was calculated based on the following morphological attributes: circularity of final chamber, apical angle, number of chambers, chamber expansion rate, umbilical view area, the ratio of the final chamber area to the total area, clavateness, keeledness, biconvexity, and lobateness. Detailed explanation of each of these attributes can be found in Kelly et al.³⁷. Attributes were measured primarily from holotypes or images sourced from community-based atlas projects⁴⁸⁻⁴⁹. A table showing the interrelationship of the ten morphological attributes is presented in Supplementary Information Table 1. This shows which morphological characters co-vary; although most do not co-vary strongly, some (like the ratio of the final chamber to total test area and expansion rate) do show a linear relationship.

Test complexity was calculated to be a rough estimation of how morphologically complex each species is, starting with assigning a “simple” morphology. Because describing any morphology as “simple” vs. “complex” is subjective, we define the simplest form as the average of two K-Pg survivor species, *Muricohedbergella monmouthensis* and *M. holmdelensis*. We feel these are good avatars of simplicity both because they represent a basic test morphology that was common throughout the Mesozoic and Cenozoic, and because they are the ancestors of many Cenozoic lineages (which become more complex over time⁴⁹). The other important K-Pg survivor species, *Guembelitra cretacea*, is inarguably more complex based on the characteristics laid out in Table S1, and thus was not considered a useful definition of simplicity, although it also gave rise to a number of important and complex Cenozoic taxa⁴⁹. For each attribute the mid-point between *monmouthensis* and *holmdelensis* was subtracted, then we took the absolute value of the result. Each attribute was then standardized to a scale of 0-1. Lastly, attributes were added together for each species, providing a score of the difference of each species from our pre-defined ‘simple’ survivor taxa. This essentially describes the disparity between all other taxa and the average of these two survivors. A principal component analysis, though analytically more complex, demonstrates similar results (see Supplementary Information).

The mean and median complexity of all species within our study interval are reported in Figure 1B. All timeseries were calculated in 250 kyr bins. For mean Test Complexity / Diversity, mean complexity was calculated as a timeseries, as was diversity, then divided. Code can be found at [Github.com/Fraass](https://github.com/Fraass).

Foraminiferal trophic strategies are based on those reported by various authors^{3,49-50} as well as the online database Mikrotax (<http://www.mikrotax.org/pforams/>⁵¹). Generally, spinose foraminifera can be identified by careful microstructure examination for the presence of diagnostic

spine holes⁵. Symbiont-bearing planktic foraminifera are commonly identified by the stable isotopic signature of their test tend to have tests relatively enriched in ¹³C, caused by the effect of algal photosymbionts on the microhabitat from which the foraminifer precipitates its calcite shell and relatively depleted in ¹⁸O, indicating a shallow water habitat⁵². Species with neither of these indicators, commonly referred to as microperforate or smooth normal perforate, are observed in the modern ocean to be mainly herbivores, feeding on phytoplankton and detritus⁵.

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Author Contributions Both authors contributed to data interpretation, figure plotting, and writing and editing the manuscript. AJF wrote the R Code and performed the morphometric measurements.

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Reviewer Information [to come]

Competing Interests Statement The authors declare no competing interests.

Data Availability Statement All data and code related to this study are available at <https://github.com/Fraass>.

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